

Acute aerobic exercise enhances pleasant compared to unpleasant visual scene processing

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ABSTRACT

Although acute aerobic exercise benefits different aspects of emotional functioning, it is unclear how exercise influences the processing of emotional stimuli and which brain mechanisms support this relationship. We assessed the influence of acute aerobic exercise on valence biases (preferential processing of negative/positive pictures) by performing source reconstructions of participants' brain activity after they viewed emotional scenes.

Twenty-four healthy participants (12 women) were tested in a randomized and counterbalanced design that consisted of three experimental protocols, each lasting 30 min: low-intensity exercise (Low-Int); moderate-intensity exercise (Mod-Int); and a seated rest condition (REST). After each of the protocols, participants viewed negative and positive pictures, during which event-related magnetic fields were recorded. Analyses revealed that exercise strongly impacted the valence processing of emotional scenes within a widely distributed left hemispheric spatio-temporal cluster between 190 and 310 ms after picture onset. Brain activity in this cluster showed that a negativity bias at REST (negative > positive picture processing) diminished after the Low-Int condition (positive = negative) and even reversed to a positivity bias after the Mod-Int condition (positive > negative). Thus, acute aerobic exercise of low and moderate intensities induces a positivity bias which is reflected in early, automatic processes.

1. Introduction

Studies that investigate the impact of physical exercise on our emotional functioning have been gaining increasing attention. Even one session of acute aerobic exercise (hereafter, *exercise*) might increase vitality, reduce stress, and promote individuals' self-confidence as they face the challenges of everyday life (for a review see: Basso & Suzuki, 2017). The positive effects of exercise have been observed not only in healthy populations but also in populations suffering from mood disorders: Exercise decreases depression, anxiety, and stress levels (Keating et al., 2018). Despite the apparent benefits of exercise on different aspects of emotional functioning, surprisingly little is known about how exercise might influence the processing of emotional stimuli and what the relevant brain mechanisms are that support this relationship. Our goal was to build a better understanding of the brain

mechanisms that underlie the relationship between exercise and subsequent processing of emotional stimuli.

1.1. Acute aerobic exercise and the processing of emotional pictures

To date, we can find only a few studies that have investigated the relationship between exercise and the processing of emotional stimuli in healthy adults (Crabbe, Smith, & Dishman, 2007; Schmitt et al., 2019; Smith, 2013; Smith et al., 2002; Tartar, Salzmann, Pierreulius, & Antonio, 2018; Thom, O'Connor, Clementz, & Dishman, 2019). These studies focused on the processing of emotional stimuli after a session of exercise and employed a similar experimental scheme. Participants attended a session of exercise and a session of "seated rest", i.e., a seated rest control condition, REST. After each session, they were presented with emotional pictures. In some of these experiments, the

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researchers collected information on participants' valence ratings about the presented picture (i.e., using behavioral measures). After the exercise as compared to after the REST condition, participants reported less unpleasant (Tartar et al., 2018) or less intense (Crabbe et al., 2007) valence ratings in response to negative pictures. In the other studies, participants reported reduced anxiety in response to aversive emotional pictures (Smith, 2013) or reduced anger in response to anger-inducing pictures (Thom et al., 2019).

In some of the studies described above, the behavioral measurements were accompanied by physiological or neurophysiological indices of emotional processing. For example, Smith, O'Connor, Crabbe, and Dishman (2002) investigated the effects of exercise on responses to emotional pictures using two measures of facial electromyography (EMG): the acoustic startle eyeblink response and the corrugator supercilii muscle activity (the "frown" muscle). As both these measures increase in response to unpleasant affective states, exercise was expected to affect EMG activity differently in response to positive, neutral, or negative pictures. However, the study showed that exercise did not affect the EMG responsiveness to emotional pictures.

Other studies have focused predominantly on neurophysiological indices, as processing of emotional pictures is strongly regulated by frontal and limbic brain regions that can be altered by exercise (Chang, Labban, Gapin, & Etnier, 2012; Fumoto et al., 2010). Although these modulating properties of exercise have been reported with respect to improvements in executive function following exercise, it is plausible that exercise might also influence neural correlates of emotional processing. Therefore, some studies have assessed the neurophysiological markers of emotional processing as revealed by electroencephalography (EEG, Crabbe et al., 2007; Tartar et al., 2018; Thom et al., 2019) or functional magnetic resonance imaging (fMRI, Schmitt et al., 2019). Crabbe et al. (2007) employed EEG in order to measure the balance of neural activation between the frontal parts of the left and right hemispheres (frontal alpha asymmetry), which is thought to reflect approach/avoidance aspects of behavior. Therefore, these EEG measurements could have provided neural evidence for tendencies to either approach or withdraw attention to pictures after exercise. However, the authors did not observe the predicted differential frontal alpha asymmetry between the exercise and the REST condition.

In another study, Tartar et al. (2018), and Thom et al. (2019) employed EEG in order to measure event-related potentials in response to emotional pictures. Event-related potentials (or event-related fields (ERFs) in the case of magnetoencephalography (MEG)) are particularly suited to provide insights into the cerebral basis of processing emotional material, as they assure excellent temporal precision of measurements (Olofsson, Nordin, Sequeira, & Polich, 2008). Two main ERP/ERF components are usually considered to reflect emotional processing in response to emotional pictures: the early posterior negativity (EPN) and the late positive potential (LPP) (Schupp et al., 2006). Whereas the EPN is a middle-latency component, typically occurring between 120 and 300 ms after stimuli onset, the LPP is a late-latency component that develops 300–500 ms after the onset of emotional stimuli. The EPN is altered by the emotional content of emotional pictures, such that emotionally arousing pleasant and unpleasant pictures result in greater EPN difference amplitudes compared to more neutral or less salient pictures, indexing more automatic processes of selective attention (Schupp et al., 2006). The LPP is commonly considered to be an ERP index of one's attention to an emotional stimulus and of the depth at which the stimulus is processed at later time interval, indexing more conscious processes like encoding relevant stimuli into working memory (Olofsson et al., 2008; Schupp et al., 2000, 2006). Overall, smaller (larger) EPNs and LPPs are usually interpreted as evidence for reduced (enhanced) emotional processing.

Given the functional interpretation of these ERP components, two studies predicted that exercise would reduce participants' EPN (Thom et al., 2019) and/or LPP amplitudes (Tartar et al., 2018) when they viewed anger-inducing or aversive pictures compared to neutral

pictures (i.e., exercise would reduce automatic selective and/or directed attention toward negative material). Yet, both studies could not find these predicted effects. Whereas Thom et al. (2019) found that exercise did not alter ERP responses to anger-evoking pictures, Tartar et al. (2018) reported a non-significant influence of exercise on the predicted interaction between the exercise session (levels: exercise, REST) and picture valence (neutral, negative). Still, post hoc analyses for the LPP in the study by Tartar et al. (2019) revealed that exercise resulted in a significantly reduced LPP for negative pictures, suggesting that processing of negative pictures might be decreased after exercise. Partial support for this result is also provided by a recent fMRI study, which tested the influence of low- or high-intensity exercise on the processing of emotional faces (Schmitt et al., 2019). The results showed that both exercise interventions increased the positive affect scale and modulated brain activation patterns induced by fearful faces in face-processing brain regions. However, as no control intervention (e.g., rest condition) was implemented, effects could have also been driven by other factors, such as task repetition.

Summing up, previous research, although limited, suggests that a session of exercise affects behavioral valence ratings related to the processing of emotional pictures. However, there is still insufficient and mixed evidence on the neural basis by which exercise affects the processing of emotional material. Although some studies suggest the exercise results in decreased processing of negative emotional stimuli, future studies are needed to further explore this relationship.

1.2. The current study

We aimed to investigate the neural signatures associated with how exercise influences the processing of emotional pictures. In light of the mixed evidence, below we present three important methodological aspects in which our study may considerably advance our understanding of the studied phenomenon.

Emotional arousal of pictorial stimuli. Although in previous studies (Schmitt et al., 2019; Tartar et al., 2018) the post hoc analyses showed decreased brain responses after exercise for negative (as compared to neutral or non-relevant) pictures, these studies either did not assess (Tartar et al., 2018) or did not show (Schmitt et al., 2019) how exercise influenced participants' responses to positive pictures. Importantly, negative and neutral stimuli not only differ in their hedonic valence (i.e., whether pictures are rated as good, bad, or rather neutral), but they also differ in their potential to evoke emotional arousal. Moreover, since a stimulus's hedonic valence and emotional arousal are strongly coupled, the described study by Tartar et al. (2018) cannot reject the alternative hypothesis, that exercise might reduce arousal reactions toward all emotionally arousing stimuli (e.g., as result of exhaustion of attention), meaning that exercise might also reduce reactions toward pleasant material. This alternative hypothesis can nicely be tested by comparing the effects of exercise on the processing of negative and positive stimuli if both valence conditions provide comparable emotional arousal (i.e., different hedonic valences but indistinguishable emotional arousal). Therefore, here we investigate differences in the processing of positive vs. negative pictures (i.e., valence biases in the processing of emotional material) using stimuli that are balanced for emotional arousal. A similar procedure of assessing biases in the processing of emotional pictures was previously employed by Tian and Smith (2011). That study utilized a dot-probe task to investigate attentional biases to emotional faces during exercise. The results showed that participants performing moderate-intensity exercise (but not high-intensity exercise) displayed a greater attentional bias toward pleasant vs. unpleasant faces and displayed a lowered attentional bias toward unpleasant faces. Although the study did not assess the acute effects of exercise and did not employ any neural measures, it suggests that exercise might indeed bias attention toward pleasant and away from unpleasant stimuli.

Spatio-temporal localization of cortical effects. Based on previous

evidence, it is not possible to infer about the dynamics of how exercise impacts the processing of emotional stimuli. Whereas fMRI is not a suitable tool to measure the temporal aspects of exercise effects, the EEG study by Tartar et al. (2018) only assessed the effect of exercise on the LPP (Tartar et al., 2018). However, analysis of the LPP component is limited: The LPP component, being a result of accumulated brain activation distributed over the cortex, does not (at least not without inverse source modeling) allow one to identify specific brain structures that could be related to how exercise influences emotional processing (Liu, Huang, McGinnis, Keil, & Ding, 2012). The LPP is also a component with a late onset, and, as such, it cannot assess the influence of exercise on earlier stages of emotional processing, especially on the EPN component (e.g., Junghöfer, Bradley, Elbert, & Lang, 2001), which has an onset between 120 and 300 ms, or on even earlier affect-modulated components such as the P1/N1 (Batty & Taylor, 2003) or the C1 (Pourtois et al., 2004), which have onsets before 100 ms. Importantly, and in contrast to how the LPP is interpreted, the emotional modulation of early visual processing prior to the LPP (< 300 ms) has been proposed to take place automatically and irrespective of stimulus detection or cognitive resources (Eimer & Holmes, 2007; Ikeda, Sugiura, & Hasegawa, 2013; Junghöfer et al., 2001; Kiss & Eimer, 2008; Pourtois et al., 2004). Thus, to understand the dynamics that enable exercise to influence the biased processing of emotional pictures, we utilize magnetoencephalographic (MEG) source space localization analysis. The excellent time resolution of this method in the millisecond range allows one to estimate the spatio-temporal dynamics of neural activity with much greater precision than fMRI measures (cf. Schmitt et al., 2019) and, therefore, allows one to study the modulatory effects of exercise on emotional picture processing at all relevant processing phases (Schoffelen & Gross, 2009).

Exercise intensity. Another potentially confounding factor in studying the relationship between exercise and the processing of emotional pictures might be exercise intensity. Considering previous work on the effects of exercise on cognition, the body of evidence suggests that exercise intensity influences cognitive performance in an inverted-U effect (Lambourne & Tomporowski, 2010). Indeed, a meta-analysis has confirmed that moderate-intensity exercise elicits greater improvements in cognition than exercise at light or high intensity (McMorris & Hale, 2012). It is unclear, however, whether a similar dose-response relationship might apply to the effects that exercise has on the processing of emotional pictures. Most studies investigating the effects of exercise on the processing of emotional pictures have not assessed the impact of different exercise intensities; instead, they have used either low- to moderate-intensity exercise (Crabbe et al., 2007; Smith, 2013) or a higher intensity of exercise (Tartar et al., 2018). The only study that did compare the effects of two different exercise intensities on processing of emotional faces (Schmitt et al., 2019) showed similar attenuating effects for both low and high intensities. As such, it is still unclear whether the effects of exercise on the processing of emotional pictures are independent of exercise intensity. Thus, an additional goal of our study was to explore whether the effects of exercise on emotional processing depend on exercise intensity: In addition to light-intensity exercise, here we also explored the effects of moderate-intensity exercise. Although our study does not allow for testing the inverted-U hypothesis, using both low- and moderate-intensity exercise will allow us to shed more light onto the role of exercise intensity in the processing of emotional pictures.

1.3. Hypotheses

We expect that exercise will affect brain mechanisms associated with the processing of emotional stimuli, mainly within the temporal and parietal cortical structures in the visual pathway. The modulation of cortical activity in these structures in response to emotional visual stimuli has been observed in previous MEG studies (Junghöfer, Winker, Rehbein, & Sabatinelli, 2017; Notzon, Steinberg, Zwanzger, &

Junghöfer, 2018; Winker et al., 2018).

Given the positive influence of exercise on emotional functioning, we expect that exercise will promote positive biases and/or attenuate negative ones. Thus, compared with the REST condition, after exercise we expect that the differences in neural reactions to pleasant minus unpleasant pictures will be more positive (or less negative), indicating a greater positive bias (or reduced negative bias). Due to the scarcity of prior research, we cannot provide specific hypotheses regarding a potential differential impact of exercise intensities; instead, we adopt an exploratory approach here. However, considering the relationship between the intensity of exercise and cognitive performance, with increased performance after moderate- compared to low-intensity exercise (Ludyga, Gerber, Brand, Holsboer-Trachsler, & Pühse, 2016), it might be expected that moderate-intensity exercise will lead to a greater positive bias (or more reduced negative bias) than low-intensity exercise.

2. Methods

2.1. Participants

Participants were recruited via advertisements posted on websites and social media portals of the University of Muenster, Germany. Inclusion criteria were as follows: 18–35 years old, normal or corrected-to-normal vision, no history of neurological or psychiatric disorders, good health, free of medication use, and no substance abuse. Two participants were excluded due to technical problems with data collection, such that the data of 24 participants were included in the analyses. None of the participants withdrew during the study, and each of them completed all testing sessions. Participants' characteristics are presented in Table 1. Each participant provided informed written consent. The experimental procedure complied with the directives of the Helsinki Declaration and was approved by the ethical boards of the University of Muenster (Germany) and the Jagiellonian University in Krakow (Poland). Participants were instructed to avoid any physical activity for 24 h prior to each experimental visit and to abstain from food for 2 h prior to each visit. For measurement of physical activity, all participants completed the BSA Questionnaire by Fuchs (2015). The questionnaire consists of three scales: 1) work and leisure time activity (working as a postman, walking or cycling to work/school, climbing the stairs, gardening, housework etc.); 2) sport activity; 3) total activity (1 + 2). Participants reported on activities they had been regularly engaged in within the last 4 weeks, providing the approximate time spent on these activities (frequency and duration in minutes). For each of the scales, we calculated a total index value in "minutes per week" (see: Table 1).

An a priori power analysis revealed that 24 participants were

Table 1
Participant characteristics (M ± SD).

	Women	Men	Total
<i>n</i>	12	12	24
Age (years)	22.66 ± 2.10	25.58 ± 4.44	24.13 ± 3.71
Height (cm)	173.58 ± 5.78	180.58 ± 5.84	177.08 ± 6.71
Weight (kg)	65.33 ± 7.98	76.29 ± 8.96	70.81 ± 10.01
BMI (kg/m ²)	21.62 ± 1.84	23.37 ± 2.32	22.50 ± 2.23
WLTPA* (min/week)	409.85 ± 126.77	333.90 ± 152.79	373.53 ± 144.87
SPA* (min/week)	267.40 ± 139.61	283.86 ± 259.08	275.27 ± 205.77
TPA* (min/week)	677.25 ± 145.18	617.77 ± 325.00	648.80 ± 249.80
HR Rest (beats/min)	61.00 ± 5.59	59.33 ± 8.65	60.17 ± 7.17

Note. WLTPA = work and leisure time physical activity; SPA = sport physical activity; TPA = total physical activity (WLTPA + SPA); BMI = body mass index; HR Rest = mean resting heart rate (measured after waking up); *as measured by the BSA Questionnaire (see Participants section for more details).

needed to detect an effect of repeated measures for within-subjects factors (effect size of $\eta^2 = 0.085$ was pulled and converted from the previous study that showed an effect of exercise on the LPP brain activity in response to negative vs. neutral pictures; Tartar et al., 2018). This estimate was calculated using G*Power software and based on a correlation of 0.6 (Cronbach's alpha) between three repeated measures from one group and an alpha of 0.05 (Faul, Erdfelder, Lang, & Buchner, 2007).

2.2. Picture perception task

The picture perception task consisted of 300 trials that included three repetitions each of 100 pictorial stimuli. The stimuli depicted 50 pleasant scenes (erotic scenes, sports, happy people) and 50 unpleasant scenes (threatening scenes, scenes of mutilation, sad people). The erotica portrayed attractive heterosexual couples engaging in normative sexual activity. Sport scenes depicted people engaging in different sports, including skiing, swimming, and track. Happy people included romantic couples, families, and children showing joy in everyday situations. Threatening scenes included people engaged in menacing or violent actions toward other people or toward the camera lens. Scenes in the mutilation category depicted graphic images of knife wounds, mangled limbs, and exposed wounds. Sad people included couples, families, and children showing sadness or suffering. As the overarching goal of our study was to investigate the impact of exercise on valence biases (negative vs. positive pictures matched in emotional arousal), we deliberately did not include neutral pictures in the procedure. This optimized our investigation of the effect of interest by limiting the additional variance of low-arousal neutral pictures. The grayscale scenes were presented at 800×600 resolution. Scene categories were balanced to be statistically equivalent in luminosity and 90% quality JPEG file size using GIMP 2.8 (www.gimp.org)¹. Stimuli were shown for 600 ms with an inter-stimulus interval randomly chosen between 1000 and 2000 ms. A red fixation dot presented in the center of the screen was continuously shown to reduce eye movements. A sample trial is presented in Fig. 1. Stimulus order was randomized with equal transition probabilities between emotional categories. Stimuli were repeated only after every image had been shown the same number of times². Visual stimulation during MEG event-related magnetic field measurement was carried out via the Psychophysics Toolbox software package (Brainard, 1997) in MATLAB (The MathWorks®; Version R2018b). Similar passive viewing paradigms have reliably evoked EPN and LPP in previous studies (Sabatinelli, Lang, Keil, & Bradley, 2007).

After completing the last session of measurement, participants rated the hedonic valence and emotional arousal of all pictures presented during the procedure using a computerized version of the Self-

¹ While some of the pictures were selected from the International Affective Picture System (IAPS; Lang, Bradley, & Cuthbert, 2008, e.g., mutilation category), our research questions necessitated more examples of the remaining scene contents than were available in the IAPS to enable us to balance luminance and complexity. The remaining pictures were selected by the Georgia Emotion Neuro-Imaging Lab of Prof. Dean Sabatinelli (University of Georgia, USA) from non-copyrighted photographs available on the internet. These pictures are consistent in composition and content with the IAPS pictures, and they will be considered for future versions of the IAPS (a more generic description of how the pictures were gathered and standardized can be found in Sabatinelli and Frank (2019)). Identical (Junghofer et al., 2017; Winker, Rehbein, Sabatinelli, & Junghofer, 2020) or similar (Farkas, Oliver, & Sabatinelli, 2020; Frank & Sabatinelli, 2019) picture sets had been used in previous studies. The picture sets are available on request from the Georgia Emotion Neuro-Imaging Lab (email: sabat@uga.edu).

² Based on previous evidence, repetition of emotional picture presentation does not lead to habituation of brain responses correlating with emotional arousal differences (Codispoti, Ferrari, & Bradley, 2006; Schupp, Stockburger, et al., 2006).

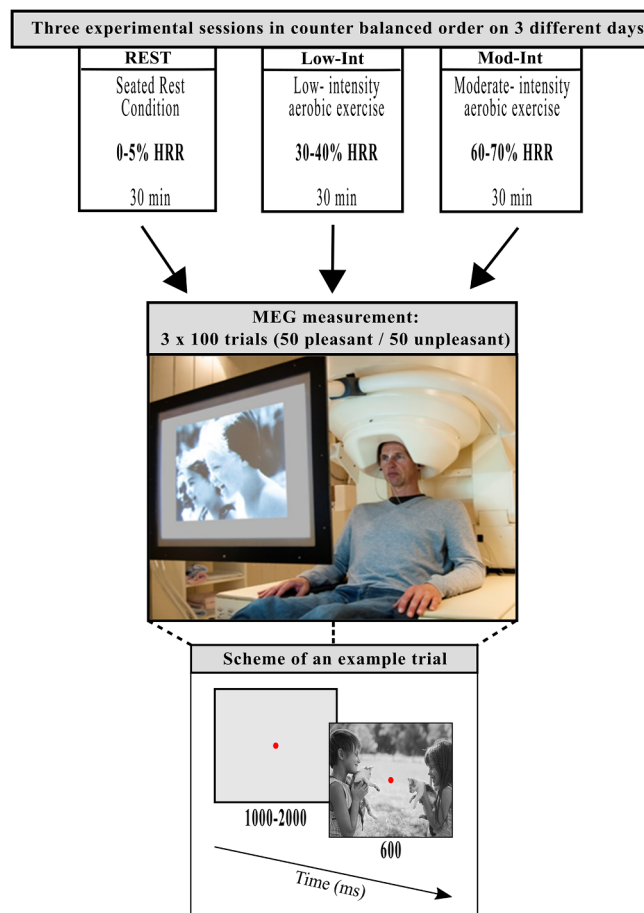


Fig. 1. The study diagram with a timeline of an example trial used in the study. The person seated in the MEG scanner released this photo but did not participate in the study.

Assessment Manikin (Bradley & Lang, 1994). The responses were given using two bipolar visual analog scales (VAS), which ranged from positive to negative (for the hedonic valence of the pictures) and from "not arousing" to "very arousing" (for the emotional arousal of the pictures). Then, responses were decoded to numerical values ranging from 0 (for the most negative/least arousing pictures) to 100 (for the most positive/most arousing pictures). The negative and positive sets of pictures differed in their ratings of hedonic valence [$M = 29.22$, $SD = 11.21$ for the negative set; $M = 81.66$, $SD = 8.45$ for the positive set; $t(23) = 20.37$, $p < 0.01$, $Cohen's d = 5.28$], and, importantly, the two sets did not differ with regard to emotional arousal [$M = 57.47$, $SD = 14.35$ for the negative set $M = 53.45$, $SD = 10.82$ for the positive set; $t(23) = 1.66$, $p > 0.05$; $Cohen's d = 0.31$].

2.3. Experimental protocols

The study consisted of three experimental protocols: two exercise sessions and one control condition session.

2.3.1. Exercise equipment.

During the first session, participants were asked to choose the exercise equipment to be used in their exercise sessions. They could choose either a bike ergometer (Daum Ergo-Bike Premium 8; Daum Electronics, Fürth, Germany) or a rower ergometer (PM4, Concept2 Inc., Vermont, USA). As some people evaluate exercising on a bike ergometer to be quite uncomfortable – which could have affected the emotional processes of interest – we decided to give participants the choice of exercising on a rower ergometer instead. In total, 4 out of 24

participants decided to perform the exercise sessions using the rower ergometer, whereas the remaining 20 participants used the bike ergometer. During each protocol, participants were equipped with a heart rate (HR) pulsometer (Polar, Finland) to measure their heart rate.

2.3.2. Experimental protocols.

We utilized two different exercise sessions: low-intensity acute aerobic exercise (Low-Int exercise) and moderate-intensity acute aerobic exercise (Mod-Int exercise). Both exercise sessions consisted of a 5-minute warm-up, a 20-minute exercise (Low-Int exercise or Mod-Int exercise), and a 5-minute cool-down phase. During the warm-up and cool down, the workload ranged between 40 and 50 W. In the case of the Low-Int exercise, participants were asked to adjust their workload to maintain the online HR (visible on their HR wrist monitor) within the limits of 30% to 40% of their heart rate reserve (HRR). For the Mod-Int exercise, participants were asked to maintain exercise intensity corresponding to 60% to 70% of their HRR. The heart rate reserve was calculated as the difference between the maximal heart rate (HR_{max}) and their resting heart rate (HR_{rest}). The maximal heart rate was calculated using the formula $HR_{max} = 211 - (0.64 \times \text{age in years})$ (Nes, Janszky, Wisløff, Støylene, & Karlsen, 2013). To determine HR_{rest}, we asked each participant to record her or his heart rate (by palpation) immediately after waking up in the morning for three consecutive days prior to the first testing session. Before taking the measurements, participants were instructed on how to measure HR_{rest} properly and were asked to count heart beats for 60 s. Then, HR_{rest} was calculated as a mean of the reported measurements. A relatively low mean standard deviation for these three measurements ($SD = 3.39$) suggests a good reliability of the measurement.

During each exercise condition, the heart rate was measured in steady-state condition. During the control condition – the seated rest condition (REST) – participants were asked to sit in the exercise room and to read sport-related magazines for 30 min. During all sessions, the participants' heart rates were measured. In the last 30 s of each session, participants were asked to rate their perceived exertion using the Borg scale (from 6 to 20 points; 6 = very, very light work; 20 = extremely heavy work) (Borg, 1982) and provide the score immediately after the session ended.

2.4. Experimental procedure

The three experimental protocols (REST; Low-Int exercise; Mod-Int exercise) were conducted on separate days, 24–72 h apart and at the same time of the day, in order to control for the circadian variation of hormones. The order of the protocols was randomized and fully counterbalanced across the final 24 participants. After finishing each of the experimental protocols, participants were escorted to an adjacent, softly lit, sound-attenuated, air-conditioned MEG chamber. After a period of approximately 10 min after the exercise protocol ended but not before the participants' HR had returned to baseline HR ($\pm 10\%$), participants were presented with the picture perception task, during which event-related magnetic fields were recorded. The schematic study diagram is provided in Fig. 1. After completing the three experimental protocols, each participant rated the pictures used in the study and was rewarded for their participation.

2.5. MEG acquisition and preprocessing

MEG measurements were conducted with a 275 whole-head sensor system (CTF Systems) with first-order axial gradiometers. Head movement and position were controlled via landmark coils positioned on the nasion and in both earlobes. MEG data were online filtered by a hardware anti-aliasing low-pass filter of 150 Hz and digitized with a sampling rate of 600 Hz.

Afterwards, offline data were down-sampled (300 Hz) and filtered with a 0.1-Hz high-pass filter (zero-phase second-order Butterworth)

and a 48-Hz low-pass filter (zero-phase fourth-order Butterworth). Trials were split into 800-ms epochs ranging from -200 to 600 ms relative to stimulus onset and baseline-adjusted using the 150 ms before picture onset (from -150 to 0 ms) as the baseline interval. Epochs with artifacts were detected and rejected using an established method for statistical control of artifacts in high-density EEG/MEG data (Junghöfer, Elbert, Tucker, & Rockstroh, 2000). This procedure detects individual channel and global artifacts and replaces artifact-contaminated sensors by spline interpolations while computing signal variance across trials as an estimate of stability of the averaged waveform. Subsequently, within each individual, epochs of visually evoked magnetic fields (VEMFs) were averaged depending on picture valence (pleasant, unpleasant) and exercise intensity (REST, Low-Int, Mod-Int). On average, 136.4 of 150 total trials for each experimental condition were used for the final average. The number of included trials did not differ across the experimental conditions (Main effect of exercise Intensity: $F(2,46) = 0.952$, $p = 0.393$, $\eta^2 = 0.040$; Main effect of Valence: $F(2,46) = 0.459$, $p = 0.505$, $\eta^2 = 0.020$; Interaction of Valence \times Intensity: $F(2,46) = 0.218$, $p = 0.805$, $\eta^2 = 0.009$). For each condition (Intensity/Valence), the mean number of remaining trials was as follows (mean \pm standard deviation): REST/Unpleasant: 137.4 ± 6.7 ; REST/Pleasant: 136.5 ± 6.4 ; Low-Int/Unpleasant: 135.1 ± 9.6 ; Low-Int/Pleasant: 134.8 ± 11.6 ; Mod-Int/Unpleasant: 137.2 ± 7.1 ; Mod-Int/Pleasant: 137.3 ± 6.7). Underlying neural sources were estimated using the L2-Minimum-Norm-Estimates method (L2-MNE, Hämäläinen & Ilmoniemi, 1994), which does not rely on a priori specification of the location and/or number of neural sources (Hauk, 2004) and, thus, is well suited to estimate distributed neural network activation. A spherical shell with evenly distributed 2 (azimuthal and polar direction) \times 350 dipoles was used as source model, and 87% of the individually fitted head radius was used as the source shell radius. Based on the averaged epochs, L2-MNE topographies were calculated for each individual, regarding both picture valences and the three exercise intensity conditions, using a Tikhonov regularization parameter k of 0.1. The resulting topographies indicated direction-independent neural source activation for the different experimental conditions.

2.6. Data analysis

Exercise intervention manipulation. To test the effectiveness of the exercise manipulation, repeated analyses of variance (ANOVAs) were conducted. The analysis was performed using SPSS Statistics version 21 (IBM, Armonk, NY, USA). Two separate analyses were conducted to assess the effect of the exercise on 1) mean heart rate during experimental protocols (levels: HR REST, HR Low-Int, HR Mod-Int) and 2) rate of perceived exertion after the experimental protocol (levels: RPE REST, RPE Low-Int, RPE Mod-Int). Follow-up pairwise comparisons were utilized with Bonferroni correction.

2.6.1. Impact of exercise on differential valence processing.

To investigate the impact of exercise on valence-specific stimulus processing (valence biases) we tested the differences of neural reactions to pleasant minus unpleasant pictures by an ANOVA with the within factor Intensity (REST, Low-Int, Mod-Int) for each estimated neural source and time point. Assessing difference scores allowed us to isolate the contribution of the neural activity that directly reflects biases in processing of emotional pictures while also reducing within-subject error variance related to day-to-day variability of measurements. Additional analyses were run to examine the independent impact of the exercise on processing positive and negative scenes and to verify whether the observed effects in biases were modulated by emotional arousal.

We applied nonparametric testing procedures similar to the cluster-mass test used for analyzing fMRI data that included correction for multiple comparisons (Maris & Oostenveld, 2007). Corresponding to

the intervals of analysis used in previous studies (Junghofer et al., 2017; Winker et al., 2018), we defined early (0–100 ms), early to mid-latency (100–200 ms), mid-latency to late latency (200–300 ms), and late latency (300–600 ms) time intervals for separate statistical analyses. Within each time interval, estimated sources were considered for further analysis only if they showed significant effects of Intensity (ANOVA) surpassing p values of < 0.05 (first level or sensor-level criterion). Temporally and/or spatially adjacent first-level significant F -values (ANOVA) of the underlying sources forming spatio-temporal clusters were then summed to constitute the cluster masses. Cluster masses were evaluated against a distribution of 1000 random permutations of the same data sets (for each permutation, the biggest identified first-level significant cluster mass was considered). Clusters were only considered significant if their cluster mass surpassed the 950th highest cluster mass of the random distribution, equivalent to $p < .05$ (second level or cluster-level criterion). If a resulting cluster reached the border of a predefined time interval, the time interval was extended by steps of 50 ms and the analysis was repeated, so that the start and end points of the resulting cluster could be estimated. If additional clusters emerged in such post hoc extended time intervals, they were disregarded. Please note that the post hoc extension of the time intervals of interest only served to better estimate the potential start and end of differential neural activity that had already been revealed as significant within the a priori defined interval. Preprocessing and analysis of MEG data was conducted using the MATLAB-based software EMEGS Version 3.1 (emegs.org; (Peyk, De Cesarei, & Junghöfer, 2011)).

3. Results

3.1. Exercise intervention manipulation

Exercise intervention showed a significant effect both on mean heart rates during the protocols [$F(2,46) = 1644.31, p < 0.001, \eta^2 = 0.99$] and on the rate of perceived exertion (RPE) after the protocols [$F(2,46) = 216.08, p < 0.001, \eta^2 = 0.90$]. Both HR and RPE measures were lower for the REST as compared with the Low-Int and Mod-Int conditions. All possible differences between REST, Low-Int, and Mod-Int conditions for both HR and RPE factors were significant at the level of $p < 0.001$. Characteristics of workloads during experimental protocols are presented in Table 2.

3.2. Impact of exercise on differential valence processing

The nonparametric ANOVA with one within-factor Intensity (REST, Low-Int, Mod-Int) that tested the difference of pleasant minus unpleasant scene processing (valence biases) revealed a single but widely distributed left hemispheric spatio-temporal cluster in the time interval between 200 and 300 ms [p -cluster = 0.02³; $F(2,46) = 12.49, p < .001, \eta^2 = 0.352$; Fig. 2A]. Post hoc nonparametric analyses of 50 ms-extended time intervals identified this cluster as becoming significant between 200 ms and 320 ms [p -cluster = 0.037; $F(2,46) = 12.333, p < .001, \eta^2 = 0.349$]. Further nonparametric post hoc tests supported the hemispheric specificity of this effect: An analysis that specifically searched for lateral symmetry (i.e., qualitatively identical effects in symmetric regions of the left and right hemisphere) did not show any right hemispheric participation. A further nonparametric analysis restricting the region of interest (ROI) to the right

Table 2

Characteristics of workloads ($M \pm SD$) during experimental sessions.

	REST	Low-Int	Mod-Int
RPE (Borg Scale)	6.33 \pm 0.48	9.5 \pm 1.69	13.96 \pm 1.89
RPE (verbal anchor)	"Very, very light"	"Light"	"Somewhat hard"
Mean HR (bpm)	64.04 \pm 7.70	110.00 \pm 7.84	148.42 \pm 5.04
%HRR	2.87 \pm 1.95	36.82 \pm 4.07	65.13 \pm 3.33
%HRmax	32.75 \pm 3.94	56.25 \pm 3.89	75.90 \pm 2.48

Note. RPE = rate of perceived exertion; HR = heart rate; HRR = heart rate reserve; HRmax = maximum heart rate; REST = seated rest condition; Low-Int = low-intensity exercise; Mod-Int = moderate-intensity exercise.

hemisphere also failed to show any effects of intensity (p -cluster > 0.971), and a direct parametric comparison of left and right hemispheric activity with a laterally mirrored spatio-temporal cluster (i.e., corresponding clusters of the left and right hemispheres between 200 and 317 ms) revealed a significant interaction of Intensity by Hemisphere [$F(2,46) = 5.274; p = .009, \eta^2 = 0.187$].

Follow-up parametric t -tests of the significant left hemispheric cluster (Fig. 2B, 2C) showed that a negativity bias at REST [$t(23) = -3.132; p = .005; d = 0.296$] changed to a slight but insignificant positivity bias after Low-Int exercise [$t(23) = 0.899; p = .378; d = 0.076$] and eventually resulted in a significant positivity bias after Mod-Int exercise [$t(23) = 3.167; p = .004; d = 0.319$]. Thus, a negativity bias for this cluster was reduced after Low-Int exercise [$t(23) = 3.521; p = .002; d = 0.823$] and was reduced even more strongly after Mod-Int exercise [$t(23) = 4.088; p < .001; d = 1.285$] as compared to REST. However, the stronger reduction after Mod-Int compared to Low-Int exercise did not reach significance [$t(23) = -1.954; p = .063; d = -0.443$]. The main effect of Intensity within this cluster was significant for positive scene processing [$F(2,46) = 3.303; p = 0.046; \eta^2 = 0.083$] but only approached significance for negative scene processing [$F(2,46) = 2.679; p = 0.079; \eta^2 = 0.011$; Fig. 2B]. The separate time courses of positive and negative scene processing for each intensity level also revealed stronger and longer-lasting effects of Intensity for positive compared to negative scene processing (Fig. 3).

A median split of the 50 positive and negative scenes into low- and high-arousal positive and negative scenes of 25 stimuli each (i.e., LowPos, HighPos, LowNeg, HighNeg) revealed convergent effects for low- and high-arousal scenes within this cluster (Low arousal: Intensity \times Val: $F(2,46) = 7.698; p = 0.001; \eta^2 = 0.251$; High arousal: Intensity \times Val: $F(2,46) = 4.455; p = 0.017; \eta^2 = 0.162$) (Fig. 4). In fact, the ANOVA of Intensity (REST, Low-Int, Mod-Int) \times Valence (Neg, Pos) \times Arousal (Low, High) revealed no three-way interaction: $F(2,46) = 1.735; p = 0.188; \eta^2 = 0.070$.

The time course of neural valence biases within this cluster showed temporally more extended differences between the Mod-Int vs. REST conditions in contrast to between the Low-Int vs. REST conditions (Fig. 2C). In fact, post hoc nonparametric paired t -tests for testing pleasant minus unpleasant scene processing in Mod-Int vs. REST identified two significant left hemispheric spatio-temporal clusters, with an earlier cluster between 137 and 220 ms [p -cluster = 0.021; $t(23) = 6.054; p = .001; d = 1.483$] and a later one between 240 and 273 ms [p -cluster = 0.026; $t(23) = 6.334; p = .001; d = 1.837$; Fig. 2D]. The Low-Int vs. REST nonparametric t -test revealed two trend-wise significant clusters, in the time intervals of 200–273 ms [p -cluster = 0.075; $t(23) = 4.178; p < .001; d = 1.162$] and 220–273 ms [p -cluster = 0.096; $t(23) = 5.751; p < .001; d = 0.982$], respectively (Fig. 3). There were no significant effects of the factor Intensity at earlier or later time intervals.

Separate cluster permutation analyses for positive and negative scenes alone did not reveal significant effects of Intensity in any time interval of interest. Additional post hoc cluster permutation analyses for the ANOVA of Intensity (REST, Low-Int, Mod-Int) of the difference of high- and low-arousal scenes across both valence conditions (HighPos&

³ p -cluster indicates the resulting p value of the a priori nonparametric cluster permutation test (i.e., if 20 of 1000 random label permutations lead to maximal cluster masses bigger than the cluster mass with correct labelling of condition within subjects the p -cluster value is 20/1000=0.02). For calculation of the effect strength, we calculated the parametric post hoc ANOVA of brain activation within the significant cluster of interest. The a priori nonparametric p -cluster values are thus bigger than the post hoc parametric p values.

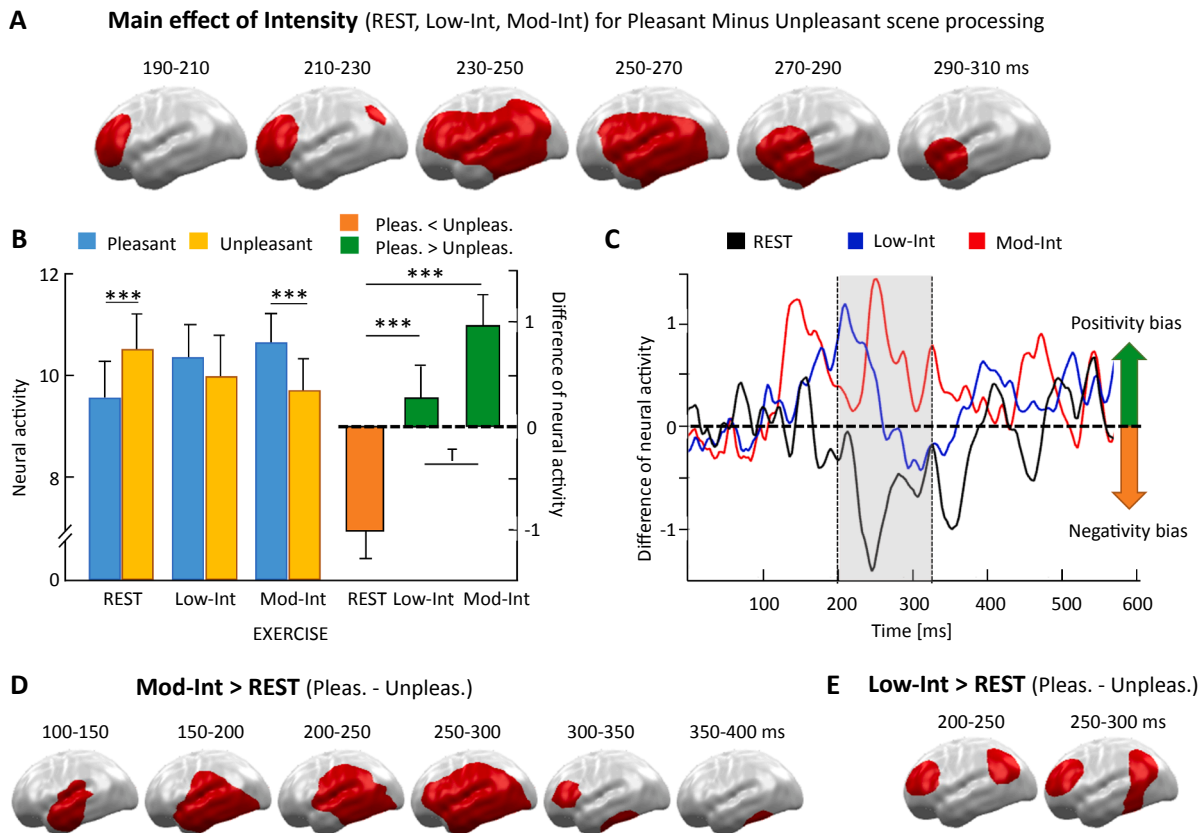


Fig. 2. An ANOVA testing the impact of exercise on emotional scene processing revealed a widely distributed left hemispheric cluster showing a negativity bias at REST which diminished after exercise at low intensity and even reversed to a positivity bias after moderate-intensity exercise. A) Spatial and temporal extent of the significant cluster. B) Neural activity within the above-shown spatio-temporal cluster during response to pleasant and unpleasant scenes as well as their respective differences for the three different activity levels. C) Time course of valence-specific processing in the cluster shown above. D) Results of post hoc nonparametric paired *t*-test comparing differential valence processing after moderate-intensity activity (Mod-Int) compared to REST. E) Results of post hoc nonparametric paired *t*-test comparing differential valence processing after low-intensity activity (Low-Int) compared to REST.

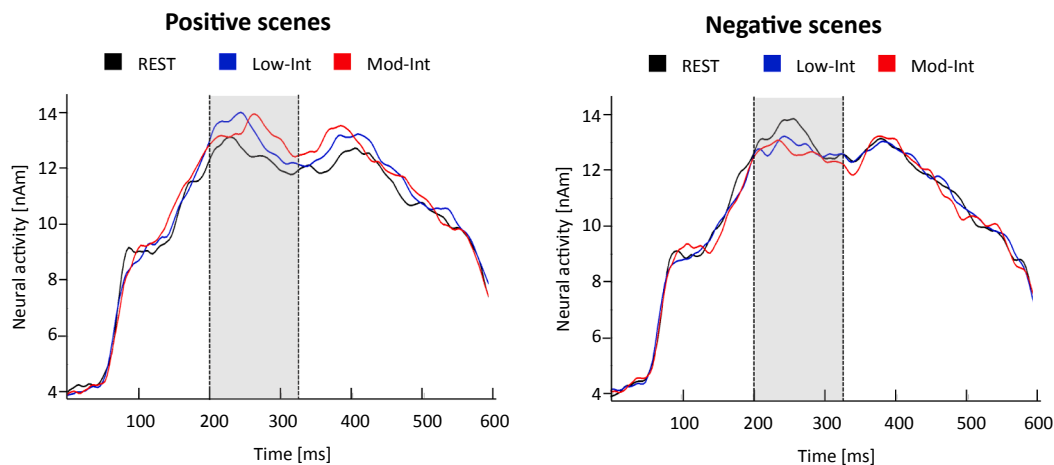


Fig. 3. The separate time courses of pleasant and unpleasant scene processing for each intensity level of exercise.

HighNeg minus LowPos&LowNeg) as well as a cluster permutation analysis of the three-way interaction (Intensity (Rest, Low-Int, Mod-Int) \times Valence (Neg, Pos) \times Arousal (Low, High)) also revealed no significant main effects or interactions in any time intervals of interest.

4. Discussion

This study addressed the influence of acute aerobic exercise (here, *exercise*) on the processing of emotional stimuli, with a particular focus

on the underlying neural mechanisms. We employed two different exercise protocols (Low-Int exercise and Mod-Int exercise) and tested their influence on valence biases (differential valence processing of emotional scenes) as revealed by MEG source space methods. A seated rest condition (REST) was employed to serve as a baseline for between-protocol comparisons. Overall, exercise had a strong impact on brain activity related to valence biases, corresponding to our hypotheses. Below we discuss the obtained results.

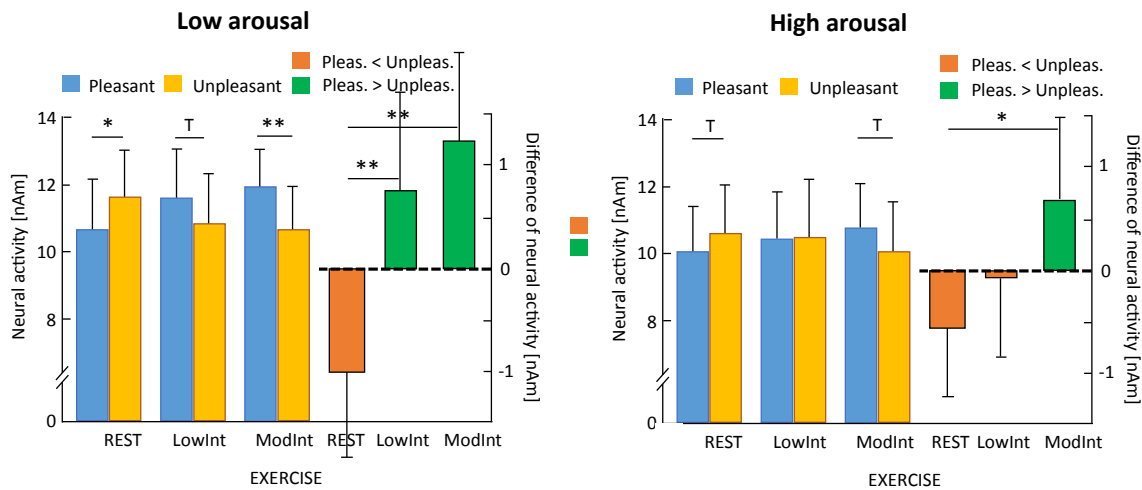


Fig. 4. Modulatory effects of exercise on valence biases for low- and high-arousal scenes.

4.1. Impact of physical activity on differential valence processing

The main analysis concerned whether and how exercise affects negative and positive biases of affective visual scene processing. The analysis revealed that both Low-Int and Mod-Int exercise strongly modulate valence biases. The strongest effects of this modulatory impact were visible in left hemispheric regions of the visual pathway in a time interval between ~ 140 to 370 ms (Fig. 2A, 2D, 2E). At REST, these regions showed a preference for unpleasant compared to pleasant scenes. However, Low-Int exercise diminished this negativity bias, while Mod-Int exercise even reversed this negativity bias into preferential processing of pleasant material (positive bias). As revealed by the additional analyses carried out independently for pleasant and unpleasant scenes, the observed bias resulted seemingly more from enhanced processing of pleasant scenes rather than reduced processing of unpleasant scenes (Fig. 3), although this difference did not become significant. Additionally, the modulatory effects of exercise on valence biases were qualitatively identical for low- and high-arousal positive and negative scenes (Fig. 4).

The timing and topography of these effects strongly indicate that exercise modulates visual pathway activity in the so-called EPN interval time between 150 and 300 ms (Eimer & Holmes, 2007; Ikeda et al., 2013; Junghöfer et al., 2001; Kiss & Eimer, 2008; Pourtois et al., 2004). The EPN is thought to relate to “natural selective attention”, which allows human brains to preferentially analyze affectively arousing stimuli over motivationally irrelevant stimuli. This processing has been found to occur rather automatically and irrespective of cognitive resources (Eimer & Holmes, 2007; Ikeda et al., 2013; Junghöfer et al., 2001; Kiss & Eimer, 2008; Pourtois et al., 2004). In light of this literature, the observed results suggest that exercise has a strong potential to bias early processes of natural selective attention, such that greater attention is directed toward positive rather than negative content.

Previous studies have systematically reported less intense negative feelings in response to emotional stimuli after exercise (Crabbe et al., 2007; Smith, 2013; Tartar et al., 2018; Thom et al., 2019). Our results might build on that knowledge, providing a possible neurophysiological background of the relationship between exercise and processing of emotional stimuli. As such, previously reported decreases in negative feelings in response to emotional pictures after exercise might be associated with biased processing of emotional stimuli by attentional processes. Such favorable biases in attention have been previously shown by Tian and Smith (2011) to occur during exercise. Our findings considerably add to these observations, showing that similar biases still persist even after the cessation of exercise.

Our results also provide a support for previous, yet limited

neurophysiological evidence on decreased processing of negative pictures after exercise (Schmitt et al., 2019; Tartar et al., 2018). By testing biases in processing of positive vs. negative material, here we proved that exercise-induced changes in processing of emotional material are not or at least are not uniquely related to the emotional arousal induced by stimuli (cf. Tartar et al., 2018). Additionally, by testing temporal aspects of the studied phenomena, we were able to show that changes in the processing of emotional pictures might result from early and rather automatic processes related to the allocation of attention (cf. Schmitt et al., 2019).

The effects of exercise on the processing of emotional pictures might be substantially modulated by exercise intensity. Yet, most of the previous studies investigating the effects of exercise on processing of emotional pictures did not assess the impact of different exercise intensities. The only study that did test this revealed that both light- and high-intensity exercise yield relatively similar changes in processing of emotional faces (Schmitt et al., 2019). In our study, the effects of exercise on the processing of emotional pictures were more robust for moderate-intensity compared to low-intensity exercise. However, and importantly, we showed that even low-intensity exercise revealed a strong valence-modulating effect, supporting the hypothesis that other low-intensity activities such as walking should provide comparable brightening effects on valence perception. By increasing the exercise intensity to a moderate level, the effects became even more profound. However, based on our data, it cannot be concluded whether a further increase in exercise intensity (to high levels) would result in additional benefits to processing emotional stimuli or would attenuate the positive effects. As such, it is still an open question of whether low, moderate, and high intensity exercise affect the processing of emotional pictures similarly to how these exercise intensities affect cognitive abilities, i.e., in an inverted-U manner (Ludyga et al., 2016). Future studies using low-, moderate-, and high-intensity exercise are needed to explore this question.

While our study provides magnetophysiological evidence for the beneficial role of exercise in processing emotional material, many neurochemical mechanisms might be involved in the observed relationship. Firstly, exercise increases endorphin release, which is often considered a reason for the elevated mood after exercise (so-called “runners’ high”). Importantly, endorphins not only impact brain areas that are involved in generating mood (Boecker, Sprenger, Spilker, Henriksen, Koppenhoefer, Wagner, Valet, Berthele, & Tolle, 2008), but they might also decrease the processing of unpleasant pictures (Ipser et al., 2013). Post-exercise benefits in processing of emotional pictures might also result from elevated levels of neurotransmitters like dopamine or serotonin. Exercise-induced increases in dopamine are

implicated in the rewarding effects of exercise (Greenwood et al., 2011), whereas exercise-induced increases in serotonin are implicated in the antidepressant effects of exercise (Babyak et al., 2000). Similar to endorphins, increased levels of these neurotransmitters have been shown to have a beneficial effect on the processing of emotional pictures (Beevers, Ellis, Wells, & McGeary, 2010; Takahashi et al., 2005). As a final example, exercise might also influence the processing of emotional pictures by modulating brain responses to stressors. Exercise seems to have acute stress-buffering effects that result from modulating the noradrenergic signaling in neural circuits that are sensitive to stress (for a review see: Sciolino & Holmes, 2012). Considering that seeing negative pictures is a mild stressor, its negative impact might be reduced via this system. Accordingly, exercise has been shown to prevent stress-induced increases in cortisol, thus affecting the activity of brain structures involved in regulating the hypothalamic–pituitary–adrenal (HPA) axis (Zschucke, Renneberg, Dimeo, Wüstenberg, & Ströhle, 2015).

All the possible neurochemical mechanisms discussed above are intensity dependent (effects are greater with increasing exercise intensity), which might explain why we observed greater effects for moderate-intensity exercise compared to low-intensity exercise. However, it should be noted that exercise also impacts the release of other neurotransmitters (e.g., acetylcholine, GABA, glutamate), other neuromodulators (e.g., endocannabinoids), and neurotrophins (BDNF, IGF-1, VEGF) (for a review see: Basso & Suzuki, 2017). Therefore, it is unlikely that the observed relationship between exercise and processing of emotional stimuli is the result of a single change in the brain's neurochemical mechanisms, such as increased endorphin release (Dishman & O'Connor, 2009). Instead, the observed effects are likely the result of complex interactions between many biochemical mechanisms that are still not understood sufficiently.

Taken together, exercise has an apparently strong impact on emotional valence processing and predominantly modulates visual scene processing in the left visual pathway within the EPN time interval toward an overall “positivity bias” which increases with exercise intensity. This effect might allow us to not only learn more about the basic mechanisms by which exercise improves emotional functioning but also gain insights into the mechanisms that support non-pharmaceutical treatment of mood disorders, especially depression. Depressed individuals (compared to healthy controls) frequently show enhanced attention toward unpleasant information and less attention toward pleasant information (Everaert, Koster, & Derakshan, 2012; Gotlib & Joormann, 2010; Mathews & MacLeod, 2005). As these biases are normalized after clinical interventions, it could be expected that exercise – having the apparent potential to decrease healthy patients' negativity bias and positive attenuation – would have a similar influence in patients suffering from depression (Everaert et al., 2012; Harmer & Cowen, 2013). As such, the presented study may be a premise for undertaking future clinical investigations in which people suffering from mood disorders are invited to participate.

5. Limitations

We acknowledge that our study does not allow for inferences about whether and how exercise modulates emotional behavior related to the processing of emotional pictures. However, as the effects of exercise on subjective ratings associated with the processing of emotional stimuli have been relatively well established by previous studies, the overarching goal of our study was to build a better foundation upon which to understand the brain mechanisms of the studied relationship. Therefore, by optimizing our procedure to observe neural effects, we resigned from introducing behavioral measurement.

As the EPN evoked by emotional scene processing is typically bi-hemispheric (Olofsson et al., 2008; Schupp, Flaisch, et al., 2006), it was quite unexpected that the bias modulation within the EPN time interval was observed only in the left hemisphere. It might be that exercise

induces some additional effects in the right hemisphere that negatively superpose with effects in the left hemisphere. In this respect, it appears important to note that the so-called ventral or task-negative attention network and the dorsal or task-positive attention system interact in an anti-correlated “pull–push”-like interaction specifically in the right hemisphere (Corbetta & Shulman, 2002; Fox, Corbetta, Snyder, Vincent, & Raichle, 2006). Of course, this interpretation is highly speculative and awaits support by future studies.

Although the sample size in our study is similar to the sample sizes of the relevant studies cited here (Schmitt et al., 2019; Tartar et al., 2018; Thom et al., 2019), future studies should consider increasing the sample size to increase the strength of the conclusions drawn from the results. Future studies should also assess the cardiorespiratory fitness of the participants to be able verify whether this variable mediates the effects reported here.

6. Conclusion

Acute aerobic exercise has an apparently strong impact on emotional valence processing in healthy control subjects. It predominantly modulates visual scene processing in the EPN time interval in the visual pathway toward a positivity bias, i.e., toward preferential processing of pleasant material and (to lesser extent) attenuated processing of unpleasant material.

CRedit authorship contribution statement

Tomasz S. Ligeza: Conceptualization, Methodology, Investigation, Software, Formal analysis, Data curation, Resources, Writing - original draft, Writing - review & editing, Visualization, Project administration, Funding acquisition. **Marcin Maciejczyk:** Methodology, Writing - review & editing. **Mirosław Wyczesany:** Writing - review & editing. **Heiko Wagner:** Methodology, Writing - review & editing. **Kati Roesmann:** Software, Formal analysis, Data curation, Writing - review & editing. **Markus Junghofer:** Methodology, Resources, Software, Formal analysis, Data curation, Visualization, Writing - original draft, Writing - review & editing, Supervision, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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